
14 Responses of Plants to Stresses of the Sonoran Desert

Thomas W Crawford, Jr

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14.1 SONORAN DESERT

14.1.1 GEOGRAPHY

The concept of a desert can be viewed differently depending upon the perspective of the beholder. Shreve considers the complexity of the concepts and definitions of “desert” by geographers, biologists, and economists. He presents an in-depth biologist’s rationale for his definition of the boundaries of the North American Desert which he divides into the Great Basin, Mojave Desert, Sonoran Desert, and Chihuahuan Desert (Shreve 1936, 1942). Later, Shreve presented a detailed description of the Sonoran Desert and its subdivisions (Shreve 1951).

The boundaries of the Sonoran Desert and its subdivisions shown in Figure 14.1 were designated based upon criteria of its vegetation and flora, and it is treated as a desert in the sense that it is a region of biological unity. Vegetation refers to characteristics of a plant community such as biomass, cover, density, dominant species, and physiognomy; whereas, flora refers to the total species composition or all vascular plant species occurring in a particular plot, area, or region of interest (McLaughlin and Bowers 1999). The word, “Sonoran” is

used to describe the region of the Sonoran Desert, because more of the area lies within the Mexican state of Sonora and because of its brevity and convenience (Shreve 1951). The map of the Sonoran Desert presented by Shreve (1951) has approximately the same boundaries as those presented in a small-scale map by Harshberger (1911) and includes seven vegetational subdivisions (Figure 14.1). The boundaries of the Sonoran Desert are sharply defined wherever the topography is abrupt; whereas, in level or rolling regions, the boundary is poorly defined and there is a gradual transition from desert types to other types of vegetation (Shreve 1951).

While Shreve’s boundaries and subdivisions of the Sonoran Desert are the most commonly accepted, there are at least five other major attempts to define these boundaries. One includes the Mojave Desert as part of the Sonoran Desert, while another excludes most of Baja California from the Sonoran Desert. Twelve years before Shreve’s publication of a map of the Sonoran Desert (1951), Dice (1939) included an area defined by Shreve in 1951 as the Sonoran Desert and other areas such as the Mojave Desert and Imperial Valley of California in a larger area that he named the Sonoran Biotic Province. Shreve’s and other delineations of the boundaries of the Sonoran Desert and its subdivisions are evidence of the

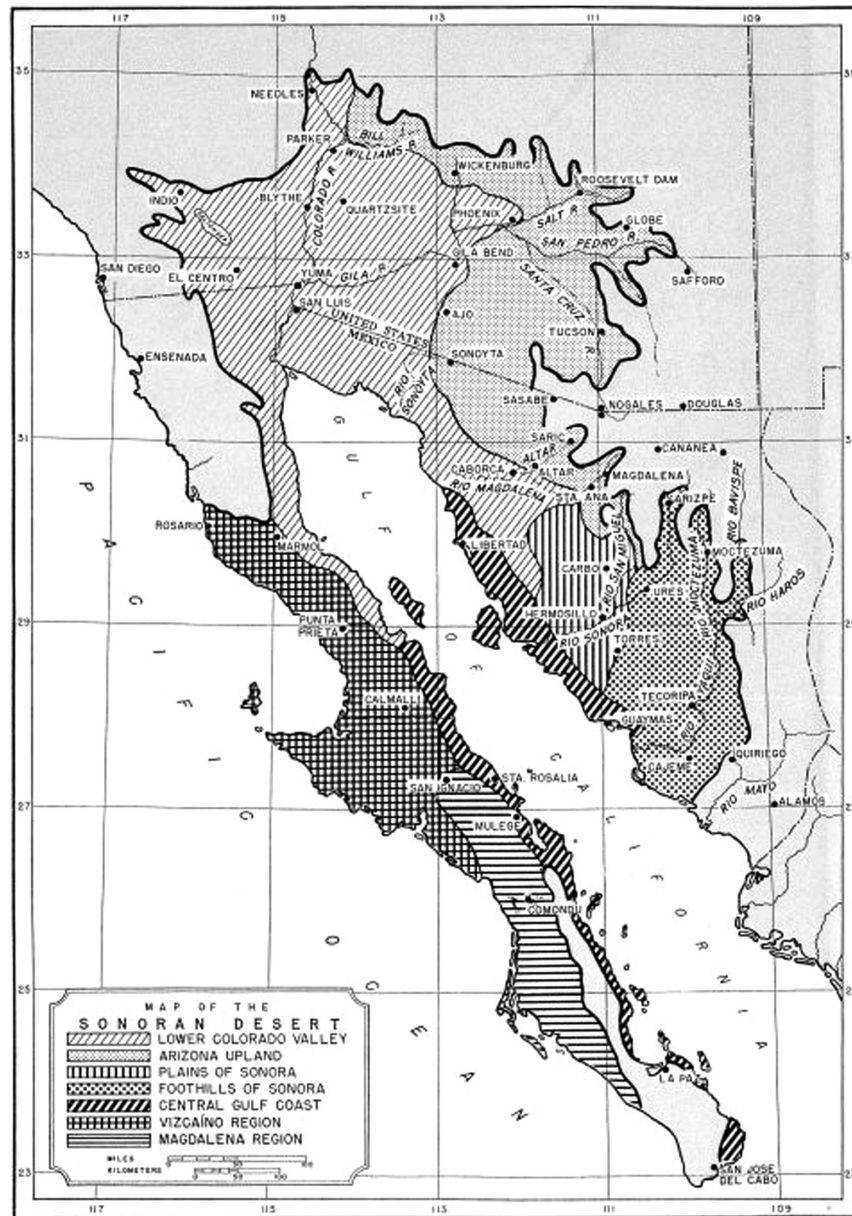


FIGURE 14.1 Map of the Sonoran Desert (Shreve 1951).

Courtesy of the Carnegie Institution for Science.

difficulty of defining precise boundaries in a geographic area with a great diversity of both geography and biota (Dimmitt 2000).

Another means of defining the boundaries of the Sonoran Desert is by using the abiotic “aridity index” of Emmanuel de Martonne (de Martonne 1926). This index is calculated for various locations, based upon annual values of precipitation in mm and temperature in °C. The general outline of the Sonoran Desert is shown in a map of the world composed in 1942 by de Martonne using the index of aridity (de Martonne 1942). Using annual data for precipitation and temperature that vary from year-to-year as a basis for calculating the index of aridity using de Martonne’s formula would result in changes in the boundaries of the Sonoran Desert

from year-to-year. Boundaries of the Sonoran Desert determined using the aridity index would result in the area of the Sonoran Desert expanding, joining with the deserts of Nevada and Chihuahua, and occasionally with the Salt Lake Desert, whereas in wet periods the Sonoran Desert would contract (Ives 1949).

The area of the Sonoran Desert as defined by Shreve based on plant communities and flora is approximately 310,361 sq km (119,370 sq mi), and parts of the desert are within four states: Sonora (126,256 sq km, or 48,560 sq mi), Baja California (62,670 sq km, or 24,104 sq mi), Arizona (105,404 sq km, or 40,540 sq mi), and California (16,031 sq km, or 6166 sq mi). Elevations in the Sonoran Desert range from sea level to 915 m (3000 ft), except for a narrow band of land along

its eastern edge in Arizona and in northern Sonora, where it is as high as 1050 m (3450 ft). Mountain ranges, so-called “Sky Islands,” are found within 70% of the Sonoran Desert in what is called basin-and-range topography, and mountain ranges border the Sonoran Desert, rising gently or abruptly from its borders, except along 1) the line of separation from the Mojave Desert between Needles and Indio, California, 2) the line of separation from the Cape Region on the Pacific side of the tip of Baja California, and 3) the line between desert and thorn forest in southern Sonora (Shreve 1951).

At elevation increases, ascending above about 1000 m elevation in the mountains, or Sky Islands, within the basin-and-range Province of the Sonoran Desert, there is a transition from one vegetational community to another. A good example of these transitions from Sonoran Desert vegetation is in the Santa Catalina Mountains north of Tucson, Arizona. At the foothills of the Santa Catalina Mountains is the Sonoran Desert Scrub plant community. Ascending the mountain, the following plant communities are encountered in sequence from approximately 1000 to 3000 m above sea level: desert grassland, open oak woodland, pine – oak woodland, pine – oak forest, pine forest, montane fir forest, and subalpine forest (Whittaker and Niering 1965). The present chapter focuses mainly upon Sonoran Desert vegetation from sea level to approximately 1000 m above sea level.

14.1.2 CLIMATE

Of the four deserts in North America – Great Basin, Mojave, Chihuahuan, and Sonoran – the Sonoran Desert is the wettest and hottest and may be the most botanically diverse desert in the world (Shreve and Wiggins 1964). Annual rainfall ranges from less than 50 mm in the Lower Colorado River Valley subdivision of the Sonoran Desert to 250 mm annually in the Plains of Sonora subdivision (Turner and Brown 1982). A major factor driving variations of rainfall from year-to-year is El Niño–Southern Oscillation (or ENSO, El Niño, and La Niña). In their study of ENSO using remote sensing and meteorological data, Zolotokrylin and others (2016) concluded that ENSO and late spring rainfall in the Sonoran Desert are related to different vegetation responses that depend on soil moisture induced by below- or above-normal rainfall. Based upon their data, they assert that a conspicuous characteristic of the Sonoran Desert is an immediate response of many plant species to an increase in moisture.

The climate in the Sonoran Desert includes droughts of various lengths of time, and recent research shows that since the mid- to late-1800s, there have been periods of the establishment of *Carnegiea gigantea* (saguaro) alternating with droughts during which few plants of this species germinated and became established (Conver et al. 2017). The authors see recent declines in establishment of stands of *C. gigantea* in the Sonoran Desert as being due to relatively recent, prolonged drought and higher temperatures, and they speculate that the destruction of nurse trees by widespread cutting in the Sonoran Desert in the early twentieth century has resulted in stress on small saguaro trees, diminishing establishment

of stands of the columnar cactus. Looking ahead to saguaros and rising temperatures in the twenty-first century, one bioclimatic model suggests that a 5°C increase in mean annual temperature could hypothetically shift the saguaro’s cold limit approximately 500 km northward and approximately 600 m upward in the Southwestern United States, mainly outside of Arizona by 2090 (Rehfeldt et al. 2006).

Research on global warming indicates faster rates throughout the twenty-first century, and the predicted increase in climatic warming may result in contraction of the overall boundary of the Sonoran Desert in the south-east and expansion of its boundary northward, eastward, and upward in elevation. Changes may also occur in distributions of plant species and other characteristics of Sonoran Desert ecosystems (Weiss and Overpeck 2005). Estimates of an increase of 3°C, or an average, linear rate of increase of 0.03°C yr⁻¹, during the twenty-first century have been linked to the possible elimination of approximately 60% of species on the planet (Hansen et al. 2006).

Extreme climatic events such as unusual heat waves, regional freezes, floods, and droughts occur from time to time in the Sonoran Desert. Such stressors that reduce biotic resistance can enable non-native species to more easily compete with native vegetation (Diez et al. 2012).

14.1.2.1 Temperature

Temperatures fluctuate throughout the year throughout the Sonoran Desert, and extreme maximum and extreme minimum temperatures present stress to plants of the desert. Climate change affects the Sonoran Desert, and the Sonoran Desert Inventory and Monitoring Network (SODN) monitors climatic changes using its stations at different locations in the desert (National Park Service 2007). SODN characterizes the climate where it monitors as having little precipitation along with temperature extremes, winter temperatures being mild and summers being quite hot. Mean annual temperatures in the SODN range from about 10°C at Gila Cliff Dwellings National Monument at the headwaters of the Gila River in Southwest New Mexico to more than 20°C in western portions of the Organ Pipe National Monument in Arizona. In the summer within the SODN, maximum summer temperatures regularly exceed 40°C at lower elevations (National Park Service 2007). As do extremely hot temperatures, freezing temperatures in the Sonoran Desert affect plant distribution. For example, a cold wave of extraordinary duration and intensity began on January 18, 1937, and it produced temperatures generally colder than had been experienced in 24 years (Turnage and Hinckley 1938).

Ranges of temperature in which plants are stressed in the Sonoran Desert can be represented by annual measurements of air temperature, the extreme maximum (highest daily maximum temperature of the year) and extreme minimum (lowest daily minimum temperature of the year). At Tucson, Arizona, during the 50-year period from 1968 to 2017, the annual, extreme maximum temperature was within the range of approximately 40°C (104°F) to approximately 46°C (115°F), and the annual, extreme minimum temperature was within

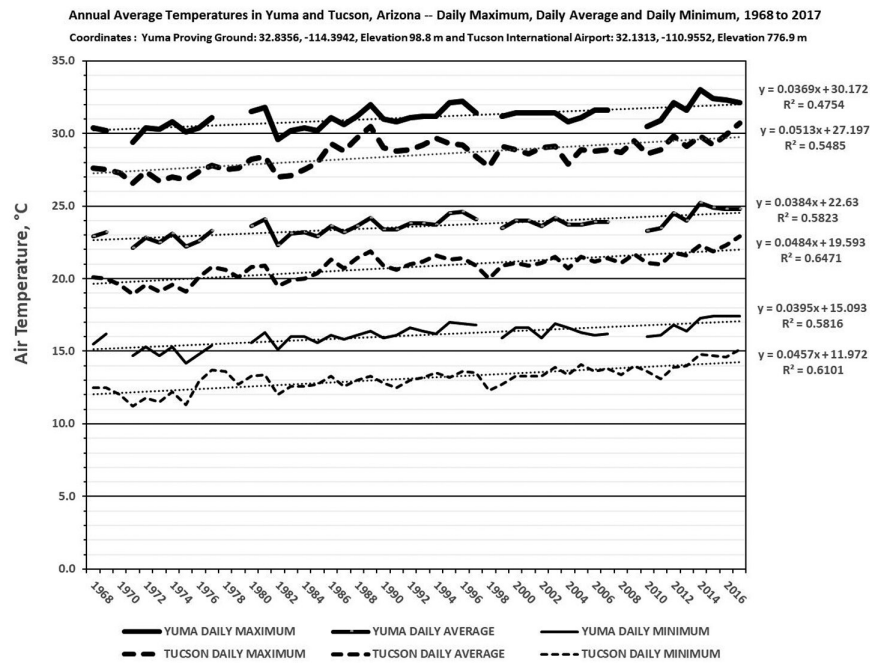


FIGURE 14.2 Annual average temperatures (°C) in Yuma and Tucson, Arizona, 1968–2017. (From NOAA/NCEI.)

the range of approximately 0°C (32°F) to –9°C (16°F). The measurement of temperature is a measurement of intensity, but both intensity and duration are critical determinants of stresses on plants of the Sonoran Desert and elsewhere.

The annual temperature data presented in Figures 14.2 through 14.4 and the monthly temperature data in Figures 14.5 and 14.6 are based upon climate data of the National Oceanic and Atmospheric Administration National Centers for Environmental Information (NOAA/NCEI) for Tucson International Airport at Tucson, Arizona and for Yuma Proving Ground located near Yuma, Arizona. The geographic coordinates of Tucson International Airport are 32.1313, –110.9552, elevation 776.9 m (2549 ft), and of the Yuma Proving Ground near Yuma, Arizona are 32.8356, –114.3942, elevation 98.8 m (325 ft).

Comparisons of annual average daily maximum, average (computed by adding the unrounded annual maximum and minimum temperatures and dividing by 2), and average minimum temperatures at Tucson, Arizona in the Arizona Upland subdivision and of Yuma, Arizona in the Lower Colorado Valley subdivision of the Sonoran Desert (Figure 14.1) show that, in general, heat stress on plants near Yuma has been greater than in the area around Tucson from 1968 to 2018 (Figure 14.2).

Also evident from the coefficients of the x term ($x = \text{year}$) of the linear regression equations of the annual temperature values of Figure 14.2 is a gradual warming trend of approximately 0.04 to 0.05°C yr⁻¹. This warming trend is evident for both locations and for all three temperature variables, the daily maximum, average, and minimum temperature. This warming trend indicates approximate rates of air-temperature increase greater than those in the Mojave Desert from 1904

to 2008 during which climate records indicate that annual air-temperature increased by approximately 2°C (36°F), or about 0.02°C yr⁻¹ (Bai et al. 2011). The global surface temperature of the earth has increased at approximately 0.2°C per decade, or about 0.02°C yr⁻¹ for three decades, as reported in 2006 (Hansen et al. 2006). Another estimate of global warming was reported in 2005 to be approximately 0.05°C yr⁻¹ (Epstein and Bloom 2005). Mean annual air temperatures are reported to have increased 0.25°C per decade, or 0.025°C yr⁻¹ Between 1949 and 2011 in the Tucson Basin (Brusca et al. 2013).

The very low values of the coefficients of determination, r^2 , of Figure 14.2 suggest that factors affecting the general warming trend are not simply the passage of time, but others not included as variables in the equations. To determine, within the period of a year, the duration of the maximal, average and minimal temperatures shown in Figure 14.2, one can refer to the website of the National Centers for Environmental Information of the National Oceanic and Atmospheric Administration which is also a source of associated monthly and daily data (NOAA/NCEI at <https://www.ncdc.noaa.gov/>).

Deeper insight into thermal stress to plants of the Sonoran Desert is evident by considering the extreme annual maximum and annual extreme minimum temperatures in addition to the average daily maximum, daily average, and daily minimum temperatures. Comparing temperatures of Tucson, for example (Figure 14.3) with those of the Yuma Proving Ground near Yuma, Arizona (Figure 14.4), it is evident that high-temperature stress on plants is greater in the environments of Yuma, compared to Tucson, but that the stress from extreme, low temperatures tends to be less at Yuma, compared to Tucson. It is notable that positive slope of the linear regression least-squares fits of the extreme annual maximum and

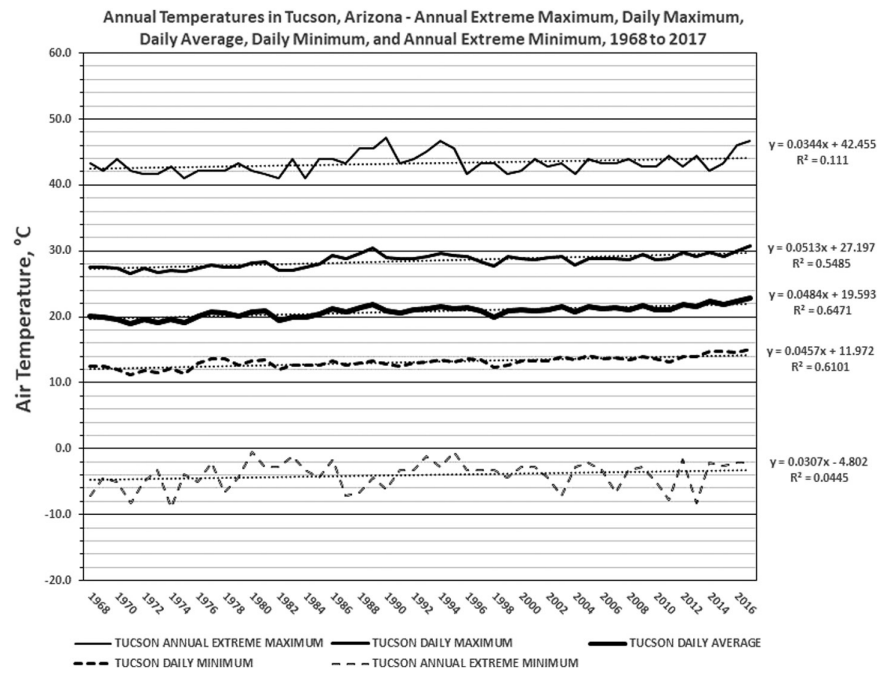


FIGURE 14.3 Annual temperatures (°C) in Tucson, Arizona, 1968–2017. (From NOAA/NCEI.)

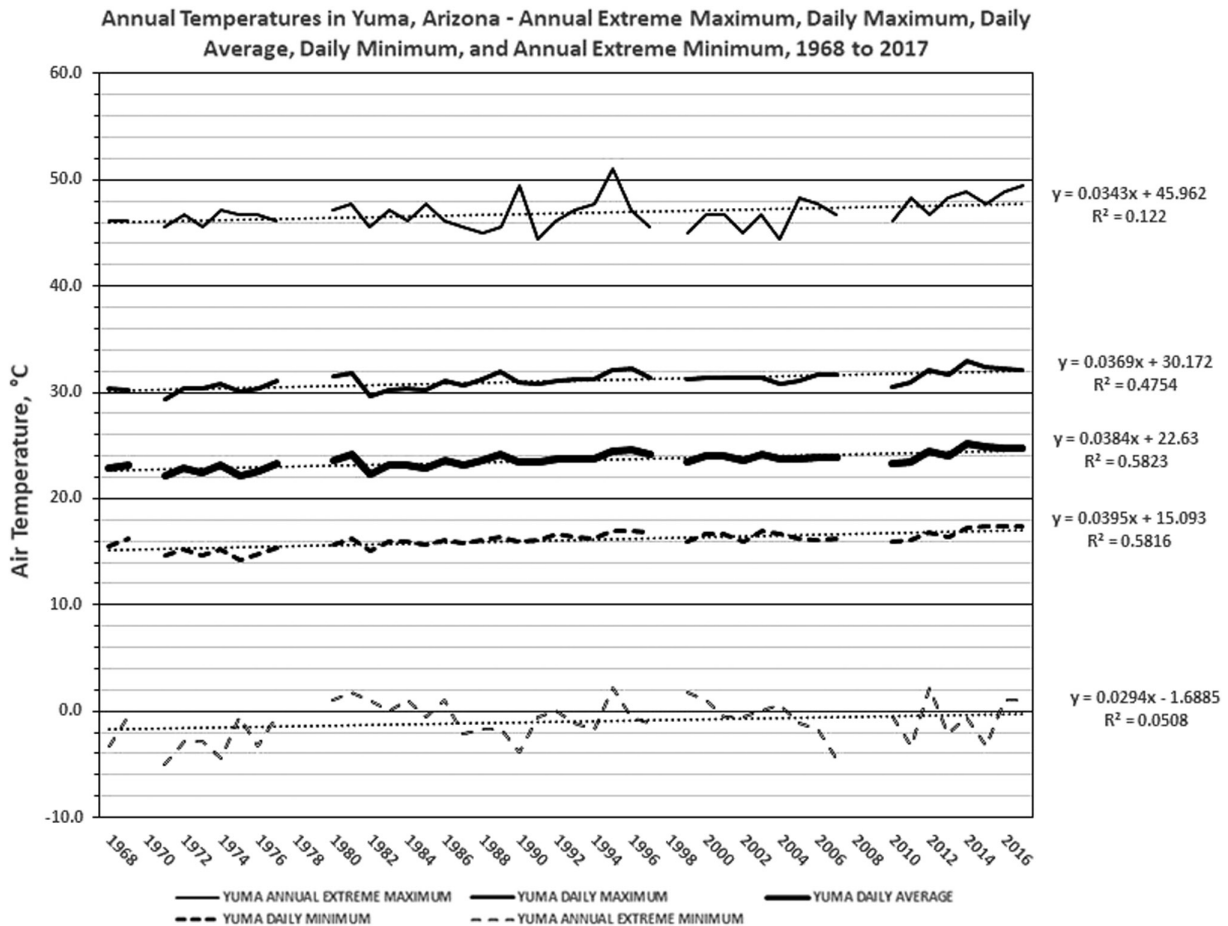


FIGURE 14.4 Annual temperatures (°C) in Yuma, Arizona, 1968–2017. (From NOAA/NCEI.)

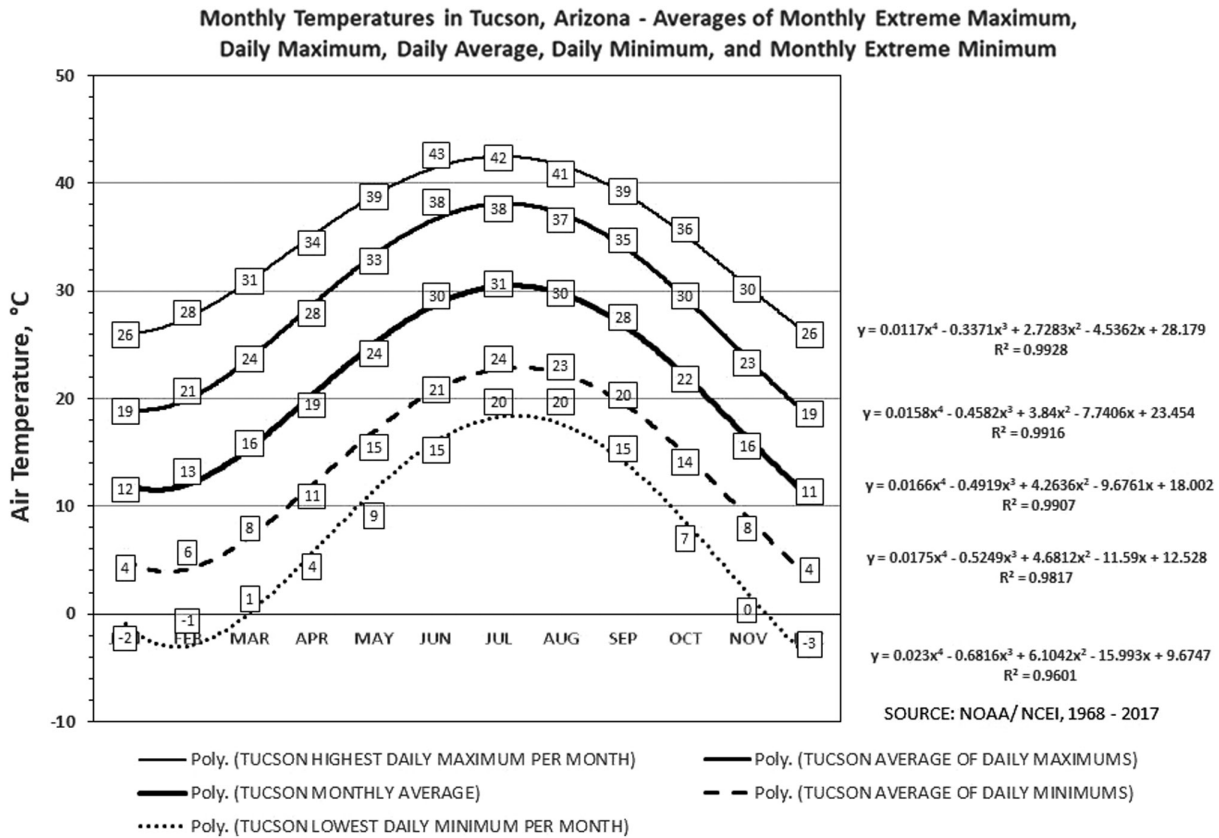


FIGURE 14.5 Monthly temperatures (°C) in Tucson, Arizona, 1968–2017. (From NOAA/NCEI.)

annual extreme minimum air temperatures data in Figures 14.3 and 14.4 are similar to those in Figure 14.2, in that they indicate an increase of both maximum and minimum air-temperature extremes. During the 50-year period of 1968 to 2017, the slight upward trend of annual extreme air temperatures at these two locations in the Arizona Upland and Colorado River Valley subdivisions of the Sonoran Desert is about 0.03°C for extreme maximum temperature and about 0.03 to 0.04°C for extreme minimum temperature. These estimated annual rates of increase are less than the estimated rates of increase shown for annual daily maximum, average and minimum air temperature (between 0.04 and 0.05°C yr⁻¹ for the two locations during the same 50-year period. From the perspective of plant stress, it is evident from the data of Figures 14.2, 14.3, and 14.4 that climatic warming is occurring at the two sites in the Sonoran Desert and that warming trends are evident for all of the air-temperature variables depicted in the figures. There is a difference of approximately 3°C between Tucson and Yuma for the annual averages of daily maximum, average, and minimum air temperature (Figure 14.2) during the 50-year period of 1968–2017.

The gradual, annual increase in thermal stress during the summer on plants (and animals) at the two locations, Tucson and Yuma, Arizona, in the Sonoran Desert during this 50-year period (Figures 14.2, 14.3, and 14.4) presents a gradually selective trend of increasing pressure on plants

with differences almost imperceptible from year-to-year. Increasing temperatures in the mountains within the Sonoran Desert have been found to enable some plant species to expand their flowering range uphill. Of 93 species that shifted their range significantly during a 20-year period as temperatures increased, most were perennials (Cohn 2009). Thus, the trend of increasing air temperatures at higher elevations can diminish the cold stress on plants, and particularly perennial plants, in the Sky Islands of the Sonoran Desert.

Botanists have found large numbers of dead creosote (*Larrea tridentata*) plants along the northern edge of their range, probably indicating death from low temperatures; moreover, heavy snowfall can completely flatten creosote plants (Shreve 1940). Increases in extreme, minimum temperatures during the winter, as shown by the data for Tucson and Yuma (Figures 14.3 and 14.4), reduce stress for some plants and may enable them to increase northward of the geographic area in which they can grow. Laboratory simulations with *C. gigantea* and several other columnar cacti to study morphological changes with latitude indicate that the northern limit for *C. gigantea*, *Lemaireocereus thurberi*, and immature stems of *Lophocereus schottii* may be determined by the low temperatures causing freezing damage to the stem apex (Nobel 1980).

More evident than the subtle increases in temperature that occur year-to-year are changes in temperature that occur

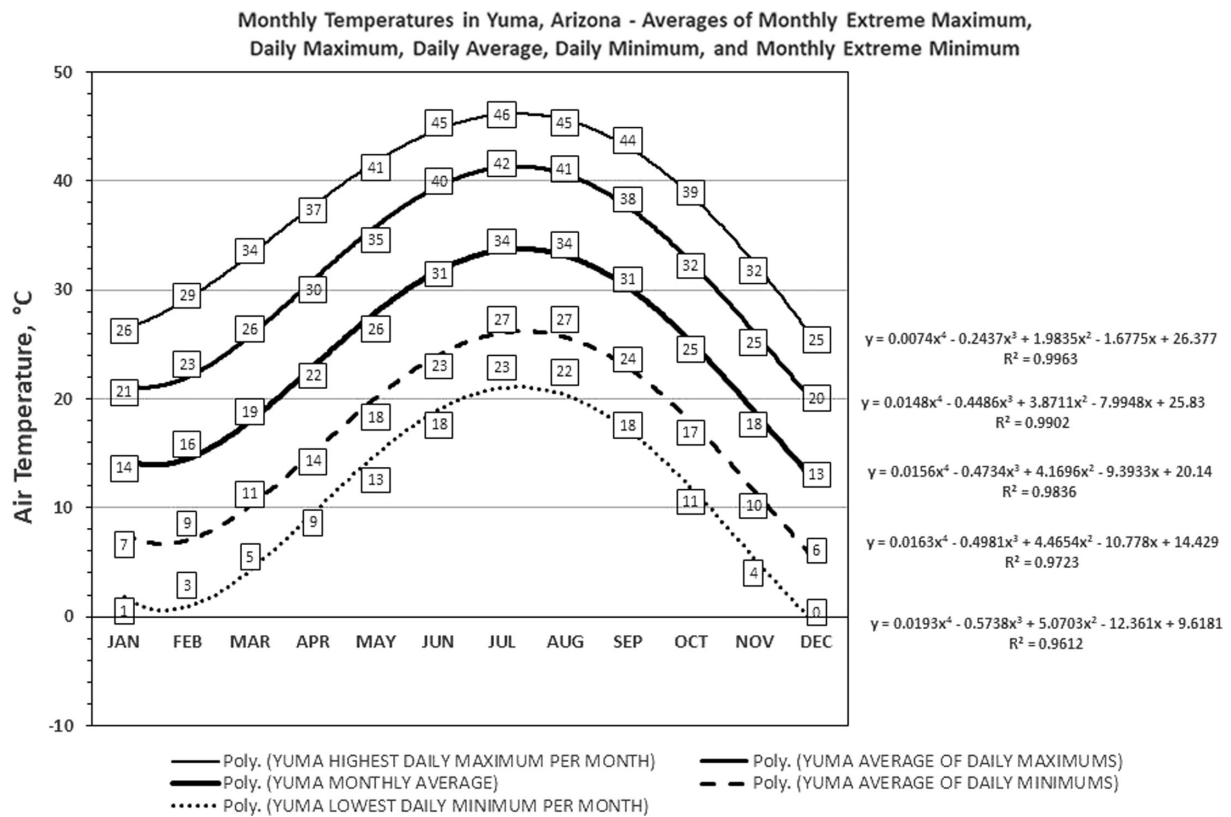


FIGURE 14.6 Monthly temperatures (°C) in Yuma, Arizona, 1968–2017. (From NOAA/NCEI.)

from month-to-month. Based on monthly temperature data of NOAA/NCEI for the 50-year period, 1968 to 2017, least-squares fits to the data are presented on a monthly basis using regression equations and mean values for Tucson (Figure 14.5) and Yuma (Figure 14.6) to show seasonal fluctuations in temperatures.

The most common temperatures experienced by plants of the Sonoran Desert in these two examples range between the average maximum and average minimum for each month, with average, exceptional extremes for each month indicated by the highest daily maximum and the lowest daily minimum for each month. Least-squares curve-fitting was done using mean values of each of the five variables for the period of 1968–2017. On a monthly basis, heat stress is greatest during June, July, and August in Tucson and Yuma and their environs, and, as is evident with the annual temperature data (Figures 14.2, 14.3, and 14.4), Yuma is warmer month-to-month than in Tucson.

Soil temperatures in the Sonoran Desert vary with depth. Temperature fluctuations at the soil surface are controlled by atmospheric conditions as well as by soil characteristics such as color and moisture-holding capacity.

14.1.2.2 Rainfall

Rainfall in the Sonoran Desert reduces the stress that arises from solar radiation that causes water to move to the atmosphere directly from soils by evaporation and indirectly

through plants by the process of transpiration. Between 1960 and 2010, the Sonoran Desert experienced a drought, with a 25 to 40% decrease in precipitation (Defenders of Wildlife 2010). Rainfall in the Sonoran Desert varies substantially in a two-dimensional sense, ranging from less than 100 mm per year to between 400 to 500 mm per year, depending upon location (Figure 14.5). Considering rainfall patterns at Yuma, Arizona, in the Colorado River Valley subdivision and Tucson, Arizona, in the Arizona Upland subdivision of the Sonora Desert, Figure 14.7 indicates annual rainfall within the range of 50 to 100 mm at Yuma and approximately 300 mm at Tucson. The isolines of “normal” temperatures of Figure 14.7 are based upon interpolated precipitation data from specific weather stations throughout the Sonoran Desert (Turner and Brown 1982) lack a temporal perspective other than the isolines being annual estimates of precipitation.

Precipitation data from the climate data of NOAA/NCEI referred to in Section 14.1.2.1 indicate substantial temporal variability of annual rainfall, during a 50-year period, in the context of the spatial variability of two locations, Tucson and Yuma, during the half-century from 1968 to 2017 (Figure 14.8). By virtue of Tucson’s location to the east of Yuma and Tucson’s higher elevation, namely 777 m (2549 ft), compared to 99 m (325 ft) at Yuma, Tucson receives more rain than Yuma. The differences in precipitation at Yuma cannot be calculated for 7 years lacking data for the Yuma Proving Ground (1978, 1979, 1980, 1982, 1998, 2008, and 2009). The small amount of

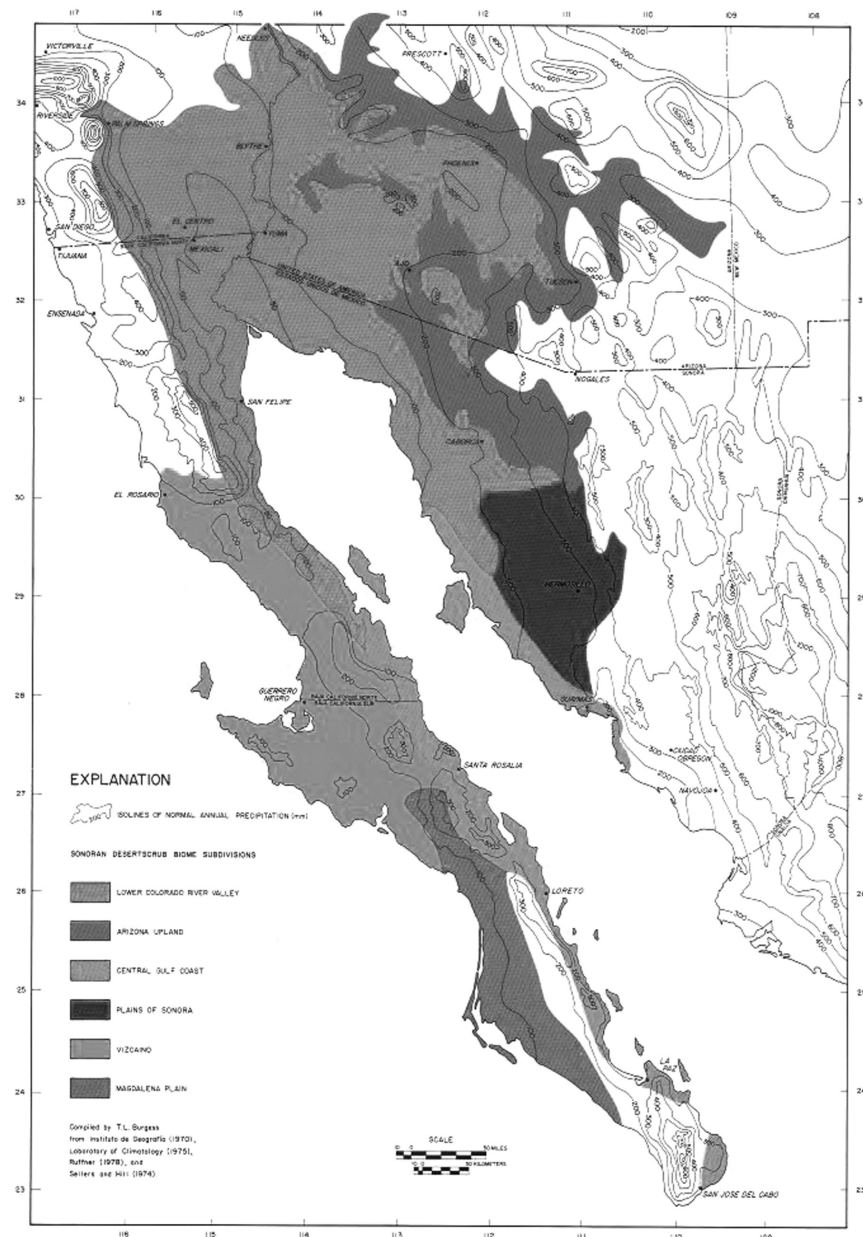


FIGURE 14.7 (See color insert.) Map of the Sonoran Desert with isolines of normal annual precipitation (mm) (Turner and Brown 1982). Courtesy of the Boyce Thompson Arboretum.

precipitation in the environs of Yuma is far more stressful to native vegetation, compared to the relatively abundant rainfall in Tucson. In the map with isolines for the Sonoran Desert (Figure 14.7), Tucson is located in between lines representing 200 and 300 mm of annual rainfall. Fifty years of NOAA/NCEI data for Tucson (1968–2017) show that there were 8 instances of annual rainfall less than 200 mm, 20 instances of annual rainfall greater than 200 mm, but less than 300 mm, and 22 years in which annual precipitation was greater than 300 mm (Figure 14.7). The NOAA/NCEI database with 43 years of data for the Yuma Proving Ground between 1968 and 2017 indicates that there were 9 years in which annual precipitation was less than 50 mm, 19 years during which annual rainfall was greater than 50 mm and less than 100 mm, and

15 years in which annual rainfall was greater than 100 mm in Yuma. The NOAA/NCEI data complement the map showing spatial aspects of rainfall distribution in the Sonoran Desert by providing insight into temporal variability of precipitation at various locations in the desert. Yuma, Arizona, is the location of the production of 90% of the leafy vegetables produced in the United States from November to March (<http://arizonaexperience.org/land/yuma-county-americas-winter-vegetable-capital>), and this is because vegetable production is dependent upon irrigation using water from the Colorado River.

Comparing annual precipitation at two locations, Yuma in the Lower Colorado Valley subdivision and Tucson in the Arizona Upland subdivision, there are both annual spatial and temporal differences during the period from 1968 to

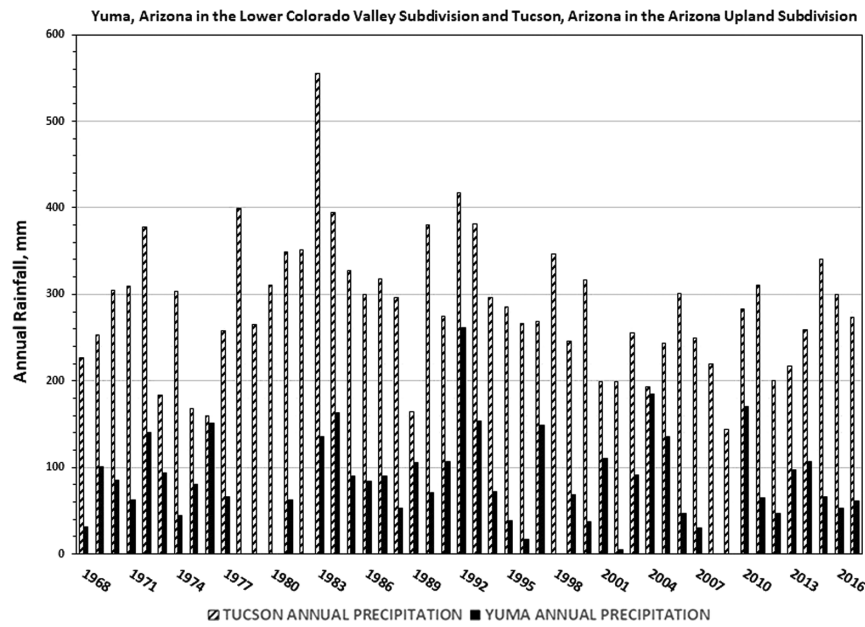


FIGURE 14.8 Annual rainfall (mm) at locations in two vegetational subdivisions of the Sonoran Desert, 1968–2017. (From NOAA/NCEI.)

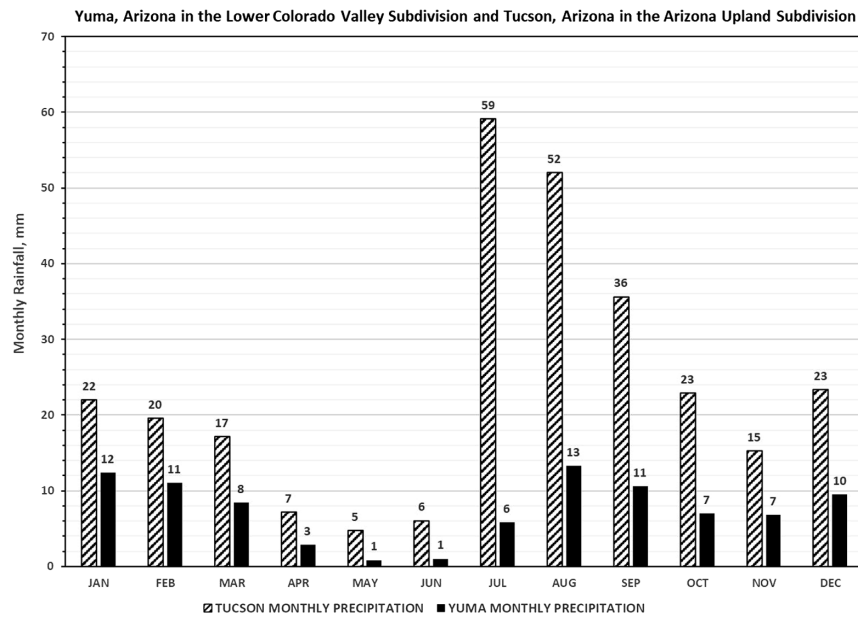


FIGURE 14.9 Average monthly rainfall (mm) at locations in two vegetational subdivisions of the Sonoran Desert, 1968–2017. (From NOAA/NCEI.)

2017. The stress on plants due to relatively little rainfall in the Lower Colorado Valley is evident (Figure 14.8), compared to the relatively abundant rainfall in the Arizona Upland subdivision of the Sonoran Desert.

A key factor in understanding moisture stress of plants in the Sonoran Desert is to understand the cyclic, temporal aspects of precipitation within the timeframe of a year. A prominent feature of many parts of the Sonoran Desert is bimodal rainfall, divided into two seasons. Regional, extra-tropical storm systems in the winter bring rain throughout

desert, but its distribution is geographically uneven, falling more in the northeastern part. In the summer, wind directions shift, bringing monsoon rains in localized, convective thunderstorms, mainly to the south-east part of the desert (Medeiros and Drezner 2012). Monthly precipitation data for Tucson and Yuma (NOAA/NCEI 50-year dataset) show clearly that there is intense, annual moisture stress in April, May, and June (Figure 14.9).

Although more rain falls every month in Tucson, compared to Yuma, there is an annual, bimodal precipitation pattern at

both locations. In their “Sonoran Desert natural events” calendar, Hanson and Hanson (2000) define five, rather than four seasons:

- Winter – December, January, early February
- Spring – late February, March, April
- Foresummer Drought – May, June
- Summer Monsoon – July, August, Early September
- Fall – September, October, November

Clearly, during May and June, the annual foresummer drought, stress from minimal precipitation is a major factor in the Sonoran Desert, as indicated by rainfall data for Tucson, in the Arizona Upland subdivision, and Yuma in the Lower Colorado Valley subdivision of the desert.

14.1.3 SOILS

Soils are derived from weathering of underlying rocks in the Sonoran Desert that results less from disintegration of the rocks by freezing temperatures and expansion of water, cracking the rock, but more from disintegration of rocks with surface temperatures of up to 65°C (150°F) to 70°C (160°F) that are weakened when rainwater of 15°C (60°F) to 21°C (70°F) contacts the very hot rocks heated by the sun. Wind and water cause erosion and deposition of soil materials, resulting in large areas of alluvial soils in the Sonoran Desert (Shreve 1951). As soils have developed in alluvial deposits of the Sonoran Desert, the downward movement of clay particles can result in argillic (clay-rich) horizons, and in many locations, calcium carbonate has been deposited within soils as water containing calcium and bicarbonate ions have moved downward (McAuliffe 1999). Deposition of calcium carbonate (lime) in soils diminishes the pore space available to hold water and air, creating an edaphic source of stress on plants, and formation of lime can entrap essential plant nutrients such as copper, iron, manganese, and zinc (Crawford et al. 2008). The extreme case of deposition of calcium carbonate in what is called a calcic horizon is called “caliche” when the pore space has been completely filled with calcium carbonate, making root growth impossible.

The water-holding capacity of soils of the Sonoran Desert varies greatly, depending upon the content and distribution of sand-, silt-, and clay-sized particles throughout the soil profile. The fine-earth fraction (National Soil Survey Center 2012) of coarse-textured soils that contain relatively little silt (2–50 µm diameter) and clay (<2 µm diameter) particles but predominantly sand (50 µm to 2 mm diameter) particles holds little water, and water moves relatively rapidly downward during rainfall events. Soils of this type can become “droughty” or lacking water, causing stress to plants with relatively shallow roots. On the other hand, deep-rooted plants have an advantage in such coarse-textured soils, being able to absorb water and mineral nutrients from depths at which such soils tend to maintain higher moisture content.

14.1.4 VEGETATION

As noted in Section 14.1.1, the Sonoran Desert is defined by its plant communities. In a two-volume tome entitled *Vegetation and Flora of the Sonoran Desert*, Shreve and Wiggins (1964) present an exhaustive description, including maps, showing the distribution of plant species in the desert. It includes a smaller volume, *Part I Vegetation of the Sonoran Desert* originally published by the Carnegie Institution of Washington (Shreve 1951). Relationships between vegetation and the environment of the northern Sonoran Desert have been found in rocky uplands and alluvial flats to be influenced by slope angle, geologic substrate, and aspect. In the Organ Pipe Cactus National Monument, a nutrient gradient was also associated with differences in vegetation, with two soil characteristics, available magnesium and pH, and aspect being significant variables (Parker 1991).

14.2 STRESSES ON PLANTS OF THE SONORAN DESERT

Survival of plants in the Sonoran Desert, like the survival of plants in any ecosystem, depends upon their physiological reactions to stresses in their environment (Osmond et al. 1987). Abiotic stresses on plants in dryland conditions such as are found in the Sonoran Desert can include drought, nutrient deficiencies, high and low extremes of temperature, salinity, sodicity, and, in relatively rare cases, water-logging. Biotic stresses occur with competition for resources, such as mineral nutrients, including water, light, space and protection from herbivores, and protection from extremes of heat and cold among individual plants of the same species and plants of different species. Additional biotic stresses of plants in the Sonoran Desert are among species of plants and animals, involving such phenomena as allelopathy, parasitism, and herbivory.

14.2.1 SPATIAL AND TEMPORAL ASPECTS OF STRESS

14.2.1.1 The Horizontal Dimensions – X and Y

Stresses of all types, both abiotic and biotic can differ from place to place. The boundaries of the seven divisions of the Sonoran Desert were determined solely by “vegetation and flora” by Shreve (1951), and these plant communities result from interaction of plant genetic material (deoxyribonucleic acid, or DNA) with resources and stresses in various environments within the desert that enabled some plants to survive, while others have not. In the Sonoran Desert as a whole, geographic coordinates (latitude and longitude) can be associated with a wide range of variables associated with stresses on plants.

For example, Shreve (1951) presented a map showing the distribution of rainfall in the Sonoran Desert with 12.7-cm (5-inch) intervals based upon interpolation of rainfall data from 4 stations in California, 17 in Arizona, 16 in Sonora, and 3 in Baja California. These differences in rainfall show the stress of low rainfall to be greatest at greater longitudes at

more westerly locations selected in the desert and the stress of low rainfall to be less at lesser longitudes to the east. Using more detailed isolines of precipitation presented in his study of the spatial characteristics of the distribution of two shrubs in the Sonoran Desert, Phillips (1979) showed that mean annual precipitation was greater for three locations (Ajo, Gila Bend, and Organ Pipe National Monument in Arizona) studied between longitudes of 112°W and 113°W, compared to mean annual precipitation at two study sites located between 114°W and 115°W (Blythe, California and Welton, Arizona). Phillips determined during his study of spatial relationships between individual plants and groups of plants of *L. tridentata* (*divaricata*), or creosote, and *Ambrosia* (or *Franseria*) *dumosa*, also known as burrow weed or white bursage, that climatic variables measured had no apparent effect on the spatial relationships between individual plants. Although he found that moisture was unimportant in the plant spacing of the two species studied, Phillips did find that different size classes of shrubs tended to change from aggregated to random to regular with increasing size of individual plants, leading him to conclude that some aspects of competition may account for changing spatial patterns of distribution of the two plant species.

14.2.1.2 The Vertical Dimension – Z

The vertical dimension can be viewed at many different scales in the Sonoran Desert. Much of the Sonoran Desert is part of the Basin and Range Province that includes slightly inclined plains on which are located many hills and mountains (Shreve 1951). Elevation above sea level is associated with climatic changes, and there are montane ecosystems within the Sonoran Desert that are popularly known as the Sky Islands. These mountain ranges include a graduated sequence of vegetation types, different from that of the valleys of the Sonoran Desert, with increasing elevation going from scrub to evergreen oaks to forests of pine, spruce, and fir at the higher elevations (Shreve 1915).

The vertical dimension of ecosystems in the Sonoran Desert has many facets. For example, although air, which is a fluid, permeates soils, it is part of a matrix of water, which is another fluid, and mineral and organic solids in soils. The interface at the surface of the soil between the soil and above-ground atmosphere is a point of division between stresses to plant roots and shoots. Solar radiation in the summer creates extreme stress which is manifest in high temperatures at the soil surface. The magnitude of fluctuations of soil temperature is greatest at the surface, and the magnitude of fluctuations of soil temperature diminishes with depth (Singer and Munns 1991). While temperature fluctuations at the surface of the soil are controlled by atmospheric forcing and are independent of soil texture, as heat moves through the soil profile, there are both amplitude damping and time lag differences associated both with depth and texture. At 48-cm (19-inch) depth, for example, comparisons of four different textural classes of soil show extremes of fluctuation of temperature during a 2-day period for sand (10 to 40°C, or 50 to 104°F),

loam (~23 to ~27°C, or ~73 to ~81°F), and silt and clay (~22 to ~23°C, or ~72 to ~73°F) (Clutter 2016). Temperature stress to soil microorganisms and to plant roots in the Sonoran Desert diminishes as depth increases below the soil surface.

Intense summer monsoon storms in the Sonoran Desert mainly impact only upper soil layers due to high runoff rates and high evapotranspiration rates (Crimmins et al. 2008). As Crimmins and others (2008) also point out, evapotranspiration rates are lower in the Sonoran Desert under cool winter temperatures, a factor that partially explains why more precipitation infiltrates soils in the Sonoran Desert to greater depths than in summer. Shreve (1934) measured rainfall, penetration, and runoff of precipitation for soil at Tucson, Arizona, in the Arizona Upland subdivision of the Sonoran Desert. From year-to-year, the amounts of these three variables varied, and from month-to-month, the data reveal that runoff occurred principally from intense rainfall events during the months of June through November, with almost no runoff during the gentler, more widespread rains from December through May. Roots of grasses and forbs in the Sonoran Desert are typically shallow, and these plants respond quickly to periodic rainfall events (Crimmins et al. 2008). However, some shrubs, such as the nurse plant, burrowweed (*A. dumosa*) can have tap roots of mature plants that will vary from 1.5 to 5.5 m (5 to 18 ft) deep, depending on soil conditions. A few laterals may branch off the taproot of *A. dumosa* in the upper 46 cm (18 inches) or so, but seldom below that depth. Fluctuations in soil moisture become fewer and of smaller magnitude with increasing depth (Cable 1969).

14.2.1.3 The Fourth Dimension – Time

The temporal dimension of stresses upon plants of the Sonoran Desert ranges from long-term (years) to short-term (instantaneous to days). Long-term stresses include periodic stresses over the long-term such as recurring droughts, floods, periods of extremely high or low temperatures, and recurring stresses from herbivores, pests or pathogens. The seasonal changes in temperature and moisture due to the rotation of the Earth on its axis and around the sun subject plants of the Sonoran Desert to periodic extremes of temperature and moisture. The Drought Monitor (<https://droughtmonitor.unl.edu/>) provides maps and tabular data regarding various levels of drought that affect the United States and, in particular, Arizona. The data from the US Drought Monitor show that drought of varying severity affects parts of the Sonoran Desert on a frequent basis, in contrast to other parts of the United States that rarely, if ever, experience drought.

In the Arizona Upland subdivision of the Sonoran Desert, a bimodal rainfall pattern exists, and there are five seasons: winter, spring, dry foresummer, monsoon summer, and fall. In the dry foresummer which is generally from mid-May to June, the increasing temperature is conducive to plant growth, but a conflicting trend of less and less available water until the monsoon rains arrive severely stresses plants in the Sonoran Desert. To cope with the extreme stress due to lack of moisture between the spring and monsoon rains in July through

September, some trees of the Sonoran Desert such as *Salix* sp. (willows) and *Populus* sp. (cottonwood) survive near a constant water supply, such as a lake, pond, or perennial stream. Other tree species such as *Prosopis velutina* (mesquite) survive this periodic stress due to lack of water with deep root systems (Shreve 1915). Trees such as *Cercidium (palo verde)* sp. drop their leaves to diminish transpiration, as do shrubs such as *Fouquieria splendens* (ocotillo); these species grow more leaves when water becomes adequate during the monsoon summer and during the winter. Some columnar cacti such as *C. gigantea* change diameter during the year, having a pleat-like structure enabling them to expand to store water or to contract as water is transpired, depending upon the availability of soil moisture.

14.2.2 ABIOTIC STRESSES

14.2.2.1 Radiant Energy Stress

Hot drylands, such as the Sonoran Desert, typically receive high solar radiation and as a result have high potential evaporation rates, high diurnal ranges in temperature, low precipitation and low atmospheric humidity (Verstraete and Schwartz 1991). There are seasonal changes in radiant energy that reaches the Sonoran Desert. Differences in insolation occur in the Sonoran Desert, depending upon aspect and slope at any particular location. Water availability tends to be greater on north-facing slopes because insolation and, therefore, evapotranspiration are lower than on south-facing slopes (Yeaton and Cody 1979). Although radiation is assumed by many not to be a limiting factor in deserts, it is important to understand that stomatal behavior of plants that restricts photosynthesis to periods of low evaporativity such as in the early morning when radiation is also low may restrict access to solar radiation necessary for photosynthesis (Noy-Meir 1973).

Modification of incoming and outgoing radiation flux occurs as a result of the growth of plants in the Sonoran Desert, for example, by two species of a common tree of the Sonoran Desert, palo verde (*Cercidium*) (Lowe and Hinds 1971). Ground temperatures on bare soil and under blue palo verde (*C. floridum*) and upland palo verde (*C. microphyllum*) trees that were 3 to 4 m (10 to 13 ft) high were observed. The effective (net) incoming radiation at ground level at midday in the open was more than twice that under the palo verde, and the effective (net) outgoing radiation in the open at night was more than twice as great as that under the tree. This mitigation of extremes of temperature and evapotranspiration due to intense radiant energy in the Sonoran Desert is associated with “nurse trees” such as palo verde (*Cercidium* sp.) and mesquite (*Prosopis* sp.) that enable other vegetation under their canopies to withstand extremes of heat and cold. Two species of plants in the Sonoran Desert that benefit from nurse trees are the saguaro (*C. gigantea*) and ocotillo (*F. splendens*) (Nobel and Zutta 2005).

Shading by native vegetation of the Sonoran vegetation creates microhabitats that can affect physiological processes such as carbon fixation by other plants. Near an equinox, shading by the nurse plant, *A. deltoidea* (triangle leaf bursage), reduced by 77% the amount of photosynthetically active

radiation (PAR) received by a seedling of *C. gigantea*, reducing its predicted net CO₂ uptake by 90% compared with an unshaded seedling. In the same study, a seedling of the barrel cactus (*Ferocactus acanthodes*) located at the center of a plant of *Hilaria rigida* (a perennial bunchgrass) received 64% less total daily PAR and could fix 65% less CO₂ than could an unshaded seedling (Franco and Nobel 1989). In a comparative study of nurse plants of saguaro (*C. gigantea*), two relatively dense, leafy shrubs, triangleleaf bursage (*A. deltoidea*) and burroweed (*A. dumosa*), a shrub with a more open canopy, creosote bush (*L. tridentata*), and three large leguminous trees, upland palo verde (*C. microphyllum*), Ironwood (*Olneya tesota*) and mesquite (*Prosopis* sp.), were mapped and described in different parts of the Sonoran Desert (Drezner 2006). The study showed that saguaros are also disproportionately distributed beneath the warmer south side of their nurse in colder parts of their range. Opening the canopy structure (e.g., leaf size and density of the canopy) probably influences soil surface temperatures, amount of photosynthetically active radiation receipt, air temperature, and possibly humidity. Drezner’s measurements (2006) show that few saguaros were established far from *L. tridentata*’s base, whereas saguaros were found under a larger portion of tree subcanopies. Means by which stresses to young plants of *C. gigantea* are reduced as a result of their nurse plant associations may include increasing shade, reducing the summertime radiation load, increasing night-time winter temperatures, increasing soil moisture, and reducing herbivory (Drezner 2006).

14.2.2.2 Low- and High-Temperature Stresses

Low temperatures during the winter months in the Sonoran Desert create stress on the biota of the desert and limit the areal extent of plant species, particularly in the northern parts of the desert. Investigating cold tolerance of columnar cacti of the Sonoran Desert, Shreve (1911) reported that *C. gigantea* was capable of withstanding 19 hours of continued freezing temperature as low as a minimum of -8.3°C (17°F). He concludes, based upon his research reported in 1911, which included controlled freezing of *C. gigantea*, that none of the individuals of the species *C. gigantea* living in the Sonoran Desert at that time has endured more than 20 hours of continuous freezing. Focusing on the possible causes of death of *C. gigantea* due to freezing temperatures, Shreve reasoned that even a single day without midday thawing during a period of freezing temperatures, coupled with cloudiness that would prevent the internal temperature of the cactus from exceeding that of the air could result in the death of *Carnegiea*. Nobel (1980) found that interspecific and intraspecific morphological differences of *C. gigantea* and other columnar cacti were factors affecting the northern extent of distribution of these cacti. He found that differences in apical minimum temperatures due to the presence or absence of pubescence and spines was related to the northernmost latitude at which various columnar cacti were found in the Sonoran Desert.

In January 1937, a polar mass of cold air spread over the western United States and caused disastrous freezes in the Sonoran Desert. The freezing effects of this large air mass

were widespread, in contrast to annual, localized freezing associated with nocturnal ground inversions which are common in the Sonoran Desert. Ground inversions of air temperature are an atmospheric condition in which the temperature increases with elevation from the ground in a topographic basin up to as much as 300 m (about 1000 ft), above which the air temperature decreases with increasing elevation. These ground inversions occur on cold, clear nights and can be damaging to desert plants that grow in low areas where cold air collects. Damage to plants documented for specific plant species due to the freeze of 1937 in the Sonoran Desert includes leaves, branches, and flowers (Turnage and Hinckley 1938).

The range of the Sonoran Desert shrub *L. tridentata* is determined, in part by freezing temperatures that cause cavitation (air bubbles) to form in its vascular system. Pockman and Sperry (1997) found that minimum temperatures between -16°C (3°F) and -20°C (-4°F) completely eliminated hydraulic conductance. They also found that record (>20 years) minimum isotherms in this same range of temperatures corresponded closely with the northern limits of *L. tridentata* in both the Mojave and Sonoran deserts. More recent research indicates that with rising minimum temperatures in the Sonoran Desert with climate change, the range of *C. gigantea* may extend to higher elevations. However, while less frequent freeze events could allow saguaros to increase their range to include higher elevations, Springer and others (2015) see indications that increased fire activity related to the establishment and spread of invasive species such as buffelgrass could inhibit expansion of the range of saguaros.

Thermal limits for the survival of metabolically active tissues of vascular plants range from about -60°C (-76°F) to about $+60^{\circ}\text{C}$ (140°F) in different species, and some vascular plant tissues, such as seeds, can remain viable by tolerating an even wider range of temperature; such extreme tolerance to temperature extremes is usually greater when metabolic activity is minimal (Osmond et al. 1987). Non-succulent plants of the Sonoran Desert have adapted to extreme, high temperatures in the summer to facilitate photosynthesis. One adaptation that enables trees such as *C. microphyllum* (foothill palo verde or little-leaved palo verde) to maintain leaf temperature close to the thermal optimum of photosynthetic enzymes, 25°C (77°F) to 35°C (95°F), when ambient air temperatures can exceed that range is microphyllly, characteristic of small leaves. Small leaves and leaflets of desert plants that are smaller than those of plants growing in wetter habitats enable the desert plants to maintain leaf temperature below lethal temperatures, even without transpiration. Another adaptation to cope with the stress of high temperatures in the Sonoran Desert is the thick, silvery hair that grows on the leaves of the *Encelia farinosa* (brittlebush) in response to drought. The highly reflective, silvery coating enables the shrub to avoid lethal leaf temperatures by diminishing heating of the leaves by infrared radiation while it reduces the level of photon flux to the leaves, lowering net photosynthesis by about a half of the rate when water is adequate (Gibson 1998).

Succulents that survive in the Sonoran Desert have adapted to extremely high temperatures and commonly high

temperatures during the summer by tolerating relatively high tissue temperatures, the mean maximum tolerance being 64°C (147°F) (Smith et al. 1984). Two species of *Ferrocactus* (barrel cactus) tolerated an absolute maximum tissue temperature of 69°C (156°F). Morphological adaptation of cylindropuntia cacti growing with a thin stem enables them to achieve lower maximum tissue temperatures, compared to more massive species of cacti, and the thinner-stemmed cacti appear to be less tolerant of high-temperature stress than are cacti with larger diameters. Acclimation of high-temperature tolerances in response to increasing day/night air temperatures was common to all 14 species of cacti studied by Smith and others (1984). For example, with the increase in air temperature from 40°C (104°F) day/ 30°C (86°F) night to 50°C (122°F) day/ 40°C (104°F) night, tolerable tissue temperatures increased an average of 6°C .

Approximately 140 species of cacti native to the Sonoran Desert are perennial stem succulents (Shreve and Wiggins 1964). To cope with high temperature during the day and drought, these succulents have adapted and survived by opening their stomata primarily at night to absorb CO_2 from the atmosphere when air and tissue temperatures are lower than in the day. The CO_2 is stored using Crassulacean Acid Metabolism (CAM) and is used in photosynthesis during the day when most of the stomata of the cacti are closed, resulting in higher water-use efficiency (mass of CO_2 absorbed per mass of water lost) (Nobel and Loik 1999). The CAM photosynthetic pathway is utilized by only about 6% of plant species, all of which have low productivity. By opening their stomates in their leaves and stems at night, plants such as cacti are able to absorb five to eight times more CO_2 per unit of water lost, compared to the 94% of plant species that open their stomates in the day (Nobel 2015).

Wildfires are catastrophic stress of extremely high temperature affecting ecosystems in the Sonoran Desert. Increases in invasive species, fires, and slow recovery by native species after a fire may have effects on desert biogeochemical cycles, since in many cases after a desert fire, soil inorganic nitrogen levels are higher, and soil carbon levels are lower. The intense heat that occurs at the soil surface penetrates and kills soil bacteria near the surface (Allen et al. 2011).

The temperature extremes and trends toward the higher high, average and low temperatures at Tucson and Yuma, Arizona (Figures 14.2 through 14.6) all indicate stress on plants of the Sonoran Desert. Temperature is a primary factor affecting plant growth and productivity, and pollination is one of the phenological stages most sensitive to extremely high temperatures. Referring to the findings of Hatfield and Prueger (2015) which focused on temperate-zone crops, increasingly high temperatures in the Sonoran Desert may select for plants that shed pollen during cooler periods of the day or are indeterminate, flowering over a longer period of the growing season.

14.2.2.3 Water Stress

Primary production of desert ecosystems is limited by, among other factors, the stresses of lack of precipitation and the lack

of availability of mineral nutrients (Hadley and Szarek 1981). A general equation to express the amount of air-dry plant material produced per unit of water consumed is:

$$\text{WUE} = D / W$$

Where WUE is water-use efficiency, D is the mass (g) of dry plant matter produced, and W is the mass (g) of water used (Epstein and Bloom 2005). The water requirement of plants, expressed by Briggs and Shantz (1914), based on their experiments with many temperate-zone plant species, ranges from about 200 to 1000 g water transpired per gram of per gram of dry matter produced, corresponding to WUE of 5×10^{-3} to 1×10^{-3} or less (Epstein and Bloom 2005). Noy-Meir (1973) estimated that 25–75 mm (1–3 inches) of precipitation per year would be the minimum necessary to sustain vegetation in an arid ecosystem; he asserted that primary production above that minimum would occur with WUE of 0.5–2 mg dry weight⁻¹ g water⁻¹, or WUE of 5×10^{-5} to 2×10^{-3} for above-ground desert primary production. The range of values of WUE based on experimental data of Briggs and Shantz for temperate-zone plants, approximately 5×10^{-3} to 1×10^{-3} , is mainly greater than the range of WUE for primary production of desert plants presented by Noy-Meir (1973), namely 5×10^{-5} to 2×10^{-3} , indicating generally greater productivity for temperate-zone crops than for plants growing in a desert.

Like all deserts, the Sonoran Desert has periods of drought stress, during which the growth rate of plants is suppressed. If the content of soil water is low enough, the matric suction (osmotic potential) of the soil is said to be at “permanent wilting point,” indicating that the plant cannot regain turgidity after wilting. The internal water potential of plants in the Sonoran Desert changes both diurnally and seasonally. The shrub, *A. deltoidea* (*Franseria deltoidea*, or triangle leaf bursage) was measured to have developed water potential as low as –85 bar and demonstrated a large range of internal water potential both diurnally and annually to ensure that it has adequate water to carry out metabolic functions. The tree, *C. microphyllum* (palo verde), in contrast, has been shown to have only a slight response of changes in internal water potential both diurnally and annually, perhaps because of its deeper root system and ability to lose leaves during periods of extreme moisture stress (Halvorson and Patten 1974).

Succulents, among which are the cacti in the Sonoran Desert, survive periods of low soil moisture content by several physiological and morphological adaptations that have evolved over thousands of years. *Opuntia* sp. (prickly pear) cactus have evolved a number of characteristics to survive the paucity of water in the Sonoran Desert. Like all succulents, *Opuntia* sp. maintains low rates of transpiration and has waxy cuticles to retain large quantities of water, compared to non-succulents. *O. laevis* (smooth prickly pear) and *O. polyacantha* (plains prickly pear), when compared to corn and soybean plants displayed little water loss, low nutrient requirements for growth, slight photosynthetic activity, slow translocation, and a low transpiration rate. The low number of stomata per unit of surface area of the prickly pear (41% of the stomata

of soybean per unit area) and the thick wax cuticle of prickly pears are important factors in reducing the diffusion of carbon dioxide necessary and penetration of light into the chlorophyll-containing grana of cells where photosynthesis occurs (Chow et al. 1966).

Cacti have an additional feature, areoles, which include spines (modified leaves) and glochids (tiny spines) that repel many herbivores and act as nodes for flowers and fruit to develop. Apical spines and pubescence of some cacti such as *C. gigantea* can help protect the growing points of the cactus from freezing (Nobel 1980). Soil moisture near the soil surface is important for desert succulents, since the roots of many desert succulent species may penetrate the soil no deeper than 0.1 m (Nobel 1976, 1977).

Seedling establishment of succulents in the Sonoran Desert is heavily dependent upon adequate soil moisture and, often, the presence of nurse plants or other shelters that can reduce the evaporative loss of water from the soil. Survival of a common succulent, *Agave deserti*, in the northwestern Sonoran Desert requires unusually wet years and the protection of sheltered microhabitats of rocks or nurse plants such as *A. dumosa* or the perennial bunchgrass *H. rigida*. *H. rigida* provided shelter for young plants of *A. deserti* that had substantially greater photosynthetic area and produced much more dry weight of living and dry leaves, compared to *A. deserti* plants under microhabitats on the north side of rocks (Jordan and Nobel 1979). In a study of the barrel cactus (*F. acanthodes*), Jordan and Nobel (1981) found that the cactus germinated in late summer and that a sufficiently long growing season was required relative to the length of subsequent droughts to allow establishment. Only 8 of the 18 years studied were found to be suitable for establishment of *F. acanthodes*. In another study, Jordan and Nobel (1982) found that *F. acanthodes* and *C. gigantea* occurred in places where at least 10% of the years were suitable for seedling establishment (Jordan and Nobel 1982). Drought stress in the Sonoran Desert presents severe selection pressure on young plants, resulting in cohorts of succulents such as *A. deserti* and cacti such as *F. acanthodes* and *C. gigantea* that can survive during prolonged droughts of more than 1 year when young. The ability of very small and young saguaros (*C. gigantea*) to survive in the Sonoran Desert is enhanced by larger plants called nurses that reduce environmental stresses to young saguaros where limitations such as freezing temperatures and recurring freezes in the north, as well as very limited rainfall in the west occur (Drezner 2004a). As saguaros grow, their water storage capacity increases, and as they grow, they are increasingly able to withstand periods of drought and high temperatures (Drezner 2004b).

Differences in slope are associated with greater or lesser stresses on plants in the Sonoran Desert, since clay-sized particles tend to accumulate lower on slopes, increasing water-holding capacity, whereas areas higher on slopes tend to have lower water-holding capacity and greater runoff. This difference in soil texture in soils at higher and lower elevations results in a gradient of increasing moisture content from higher to lower areas on a slope after rainfall (Yeaton and

Cody 1979). Moisture stress in riparian areas of the Sonoran Desert is seasonal, and during the dry foresummer, most herbaceous growth in the desert upland was found to be restricted above the floodplain of the San Pedro River (Arizona, USA). In the floodplain, a permanent source of water (shallow groundwater and associated capillary water) resulted in persistence of some herbaceous species during the dry summer season. Plant species diversity at both microscale and meso-scale increased along an elevational continuum from the drier uplands to the lowest floodplains. In the winter, however, the zone of maximum microscale plant diversity shifted to the upland, due to flood-related stresses such as flood scour in the floodplain (Stromberg 2007).

Production of seeds, interception of photosynthetically active radiation and uptake of CO₂ all increase as saguaro cacti (*C. gigantea*) develop branches, and branching increases with increasing moisture. By using stepwise regression to determine which climate, vegetation and soil variables best predict branching, Drezner (2003) found that, contrary to the literature, winter precipitation, particularly from January to April, was the best predictor of branching, not summer or annual rain. A study of the long-term demographics of *C. gigantea* in the Sonoran Desert, Pierson, Turner, and Betancourt (2013) determined that across the region, saguaro regeneration rates were highest from 1780 to 1860, which corresponded to a period of wet conditions and high *Pinus ponderosa* recruitment in the highlands. They speculate that milder and wetter winters and protection from livestock grazing may account for some surges of regeneration of *C. gigantea* at some sites within the region in the late twentieth century. Reduction of stress by increased rainfall enabled populations of *C. gigantea* to increase, but as Pierson and his colleagues point out, other stress factors such as grazing, extremely high or extremely low temperatures, and the aspect of the slope on which the saguaros grow must also be taken into account to understand demographic trends.

Long-term vegetation change at the Sierra del Pinacate Reserve in Sonora, Mexico, which is within the Sonoran Desert, was correlated with climatic data. Within the MacDougal Crater during the first half of the twentieth century, various populations of *L. tridentata* declined 50–90%, and the population of *Cercidium* spp. decreased 60%, while during the same period the population of *C. gigantea* increased fourfold. There were three major establishment peaks for *C. gigantea* during the periods, 1875–1890, 1905–1915, and 1945–1949. The high mortality of *Cercidium* and *L. tridentata* was probably a result of a prolonged drought during 1936–1964 (Turner 1990). Two-dimensional distribution patterns of *Larrea* (creosote) have been found to be associated with rainfall – more rainfall resulted in more dense populations of *Larrea*. At high rainfall levels, plants of *Larrea* were found to be grouped in clumps, and at low levels of rainfall, individual plants were regularly spaced, reflecting competition for rainwater absorbed in the soil (Woodell et al. 1969).

Drought stress of mesquite (*Prosopis glandulosa*) in the Sonoran Desert was mitigated by the ability of this phreatophytic tree to absorb water from 4 to 6 m (13 to 20 ft) deep

in the soil. Other adaptations of this species which enable it to withstand the stress of a lack of moisture are an osmotic adjustment and seasonally changing stomatal sensitivity to vapor pressure deficit (Nilsen et al. 1983). Another microphyllous plant, *L. tridentata* (creosote bush), is able to conserve water partially as a result of its leaves being covered by resin. This coating that is 2 to 4 μm (0.00008 to 0.00016 inches) in thickness is in epidermal cells, reduces epicuticular transpiration and also repels herbivores (Gibson 1998). The phenological characteristics of *L. tridentata* are adapted to the waxing and waning of drought stress, since active vegetative growth precedes renewal of reproductive activity. Flower buds of *L. tridentata* emerge and are sustained when soil moisture is adequate, and differences in phenological responses studied at four locations in the Sonoran Desert appeared to be caused mainly by local fluctuations in precipitation (Abe 1982).

The characteristic of being drought-deciduous is a way that many plants of the Sonoran Desert conserve water. Examples of plants that drop their leaves (aphylly) during periods of drought are the *Cercidium* sp. (palo verdes) and *F. splendens* (ocotillo). These two species of plants that drop their leaves during periods of drought have a photosynthetic pigment in their stems and can carry out photosynthesis without their leaves. *L. tridentata* has been found to allocate more carbon and nitrogen to reproductive, rather than to vegetative tissue under conditions of drought stress, and this allocation to reproductive tissue may confer a survival advantage to *L. tridentata* under conditions of drought and high-temperature stress (Sharifi et al. 1988).

Annual plants of the Sonoran Desert survive by evading the summer drought. Leaf water potentials are high, suggesting that photosynthesis and transpiration rates of many, if not most, desert annuals are higher than in desert evergreen and drought-deciduous perennials. Root:shoot ratios of both summer and winter desert annuals are quite low, indicating, perhaps, that a relatively small proportion of the carbon fixed is used for water acquisition. The greater proportion of the carbon fixed by these annual plants appears to be used for vegetative and reproductive growth of tissue above ground (Forseth et al. 1984). Avoiders of drought are not ephemerals with a short time to accomplish vegetative growth and produce seed. Drought avoiders in the Sonoran Desert have special structural modifications to avoid water loss. These include, but are not limited to, a thick epidermis, waxy coating of the epidermis, sunken stomata, rolling of leaves during drought, and dropping of leaves during drought. Some plants that have no leaves, such as cacti (e.g., *Opuntia* spp. and *C. gigantea*), and *Euphorbia* spp. and others that lose their leaves to conserve water during drought, such as *Cercidium* spp. and *Fouquieria splendens*, have the ability to carry out photosynthesis in their stems (Ram and Gupta 1997).

14.2.2.4 Edaphic Stresses

Large portions of the Sonoran Desert contain alkaline soils, the pH of which is greater than 7. Distribution of several Sonoran Desert plant species (*C. gigantea* and several of its nurse plant species, i.e., *A. deltoidea*, *A. dumosa*,

C. microphyllum, *L. tridentata*, *Prosopis* spp., and *Olneya tesota*) has been shown to be associated with a general east–west gradient where temperature increases and precipitation decreases westwards and calcium levels, total organic carbon, particle size, and soil pH increase westward (Medeiros and Drezner 2012). The researchers of that study concluded that a gradient in soil pH probably governs the range of several species (e.g., *A. deltoidea*, *A. dumosa*, and *L. tridentata*) that were found in calcic soils in western areas, in contrast to eastern regions with lower soil pH and higher precipitation. They concluded that the distribution of the dominant species reflects a temperature–precipitation–calcium–pH gradient.

Calcium carbonate, or lime, is common in many soils of the Sonoran Desert, and low availability of phosphorus (P) in soils can limit plant growth. Controlled experiments on the effects of calcium carbonate (CaCO_3) in soils upon uptake of P by two Sonoran Desert shrubs, *L. tridentata* (DC.) Cov. and *Parthenium incanum* H. B. K. show that increasing levels of CaCO_3 inhibited the uptake or availability of P to roots of *L. tridentata* seedlings that responded with increased root:shoot ratios, increased N:P ratios in tissues and decreased specific absorption rates of P (Lajtha and Schlesinger 1988). Declining P concentrations in the tissues of *L. tridentata*, particularly in the roots, and increased root growth are interpreted by Lajtha and Schlesinger as indications of reduced P availability. N concentrations of tissues of *Parthenium* seedlings were relatively unaffected by soil CaCO_3 levels, and although P concentrations in the tissue of *P. incanum* plants were greater with the CaCO_3 -free treatment, compared to plants growing in soil with added CaCO_3 , the differences were small, and the N:P ratios were similar. The stress of an edaphic factor, low soil P availability, results in responses of at least one Sonoran Desert plant, *L. tridentata*, such as increased root:shoot and lower N:P ratios in tissues.

In a study of 99 sites in the Organ Pipe Cactus National Monument, Arizona, slope angle and soil texture were key factors in the distribution of vegetation (Parker 1991). The patterns of monthly average temperature and rainfall at the Monument are similar to the corresponding 50-year averages for Tucson, Arizona, presented in Figures 14.5 and 14.9. Soils that developed from plutonic parent material, e.g., granite, tended to be lower in magnesium and tended to be of coarser texture, compared to soils of the volcanic parent material. Slope aspect was associated with stress. South-facing slopes with greater heat stress and lower moisture availability were more stressful than north-facing slopes with soils that were cooler and moister. The study pointed to soil chemical properties as being significant factors to modify the prominent influence of water availability on patterns of desert vegetation in the Sonoran Desert.

P. velutina (velvet mesquite) in the Sonoran Desert has been shown to reduce edaphic stress by creating islands of soil fertility with higher soil organic matter, net N mineralization, net nitrification rates, and microbial biomass under the trees' canopies (Schade and Hobbie 2005). In a study of soil characteristics under the canopy of *P. glandulosa* and a non-vegetated area between mesquite trees, it was found that

under the mesquite canopy, total N, NO_3^- -N, NH_4^+ -N, organic C, NaHCO_3 -extractable PO_4^{3-} -P, and saturation-extract K^+ were significantly higher under the mesquite (Virginia and Jarrell 1983). In the same study, Na^+ and Cl^- concentrations were significantly higher in the soil between the mesquite trees. Those conducting the study concluded that most of the N in the soil under the mesquite trees had been symbiotically fixed by bacteria in root nodules of the mesquite. Foliar analysis indicated that the mesquite was excluding Na^+ , resulting in the leaf litter containing a lower concentration of Na^+ than that of the soil between the mesquite trees. The accumulation of atmospheric N in mineral and organic forms as a result of the growth of the mesquite minimized the stress of lack of inorganic N in the soils under the mesquite trees.

Saline soils in the Sonoran Desert place stress both on plants and upon soil bacteria that fix atmospheric nitrogen which becomes available for uptake by the roots of plants in the desert. Rhizobial and bradyrhizobal symbiotic, nitrogen-fixing bacteria found in the Sonoran Desert have been found to have evolved to tolerate high salinity; this tolerance of salinity may be a key factor in the ability of a host of these nitrogen-fixing bacteria, mesquite (*Prosopis* sp.), to survive in marginal, saline soils (Jenkins 2003).

14.2.3 BIOTIC STRESSES

14.2.3.1 Competition among Plants

In a field study of *L. tridentata*, Brisson and Reynolds (1994) found that competitive interactions among root systems of neighboring plants of the same species affected the arrangement of the root systems of creosote. The observed tendency of *L. tridentata* plants to reduce intraspecific root system overlap is in contrast to the extensive interspecific intermingling of root systems observed by Caldwell and Richards (1986). Roots of *Ambrosia dumosa* inhibited elongation of contacted roots of only other *A. dumosa* plants, and the apparent chemical communication among *A. dumosa* plants may be a detection-and-avoidance system to avoid the stress of competition for mineral nutrients, including water, in soil (Mahall and Callaway 1992).

Buffelgrass (*Pennisetum ciliare*) is an aggressive, non-native grass species introduced to the United States in the 1940s. This non-native grass is invasive in the Sonoran Desert and provides stress to native grass species in the Sonoran Desert by competing with and displacing the native grasses. Buffelgrass has been associated with reduced plant species diversity (Stevens and Falk 2009), and research has shown that buffelgrass may suppress germination of the seeds of some legume species by exuding allelopathic compounds (Fulbright and Fulbright 1990). The invasion success of buffelgrass is due, in part, to its ability to emerge following relatively low levels of rainfall (Ward and Smith 2006). Buffelgrass greatly increases fuel loads in the desert and increases fire which causes high mortality rates of *C. gigantea*, so buffelgrass is a threat not only to native grasses and legumes of the Sonoran Desert but also to the iconic saguaros (Drezner 2014).

14.2.3.2 Stress Relationships between Plants and Animals

Animals ranging in size from microscopic to large mammals interact with plants of the Sonoran Desert. Many interactions are mutually beneficial, such as pollination and seed dispersal accomplished by animals for the benefit of plants. Others such as herbivory of vegetative tissue of plants by animals tend to favor the animals more than the plant. Cacti are often low in protein, and mature cactus pads often contain less than 1% protein on a dry-weight basis, but their digestible-energy production per mm of rainfall is high, making them a nutritional complement to nitrogen-fixing plant species such as *Prosopis* (mesquite) (Russell and Felker 1987). *L. tridentata* experiences the stress of phytophagous arthropods that are seeking nutrients to survive. In experiments using fertilization with nitrogen, it was found that sap-sucking phytophagous insects were more responsive than leaf-chewing insects to the increased nitrogen content of *L. tridentata* bushes (Lightfoot and Whitford 1987). In the Sonoran Desert, trees of *Prosopis* spp. are stressed by *Prosopis* seed beetles, *Algarobius prosopis* and *Neltumus arizonensis*, that lay their eggs on the pods containing seeds. Females of *A. prosopis* can lay up to 300 eggs, and the females of *N. arizonensis* usually lay about 70 eggs. Once the larvae hatch from the eggs, they crawl on the pods, burrow through them and then chew their way into undamaged seeds. By damaging *Prosopis* seeds, these two pests reduce the number of viable seeds that drop from the tree to become part of the soil seed bank. In South Africa, these beetles are used for the biological control of weedy *Prosopis* trees (Klein 2002).

Birds are granivores of the Sonoran Desert and are important primary consumers as they harvest seeds. In the Sonoran Desert, resident, avian granivores include *Zenaidura macroura* (mourning dove), *Columbigallina passerina* (ground dove), *Carpodacus mexicanus* (house finch), *Lophortyx gambelii* (Gambel's quail), and *Amphispiza bilineata* (black-throated sparrow). Other resident species such as *Pipilo aberti* (*Melozone aberti* or Abert's towhee) and *Toxostoma curvirostre* (curve-billed thrasher), which, although primarily insectivorous, can consume large quantities of seeds. Migratory birds also contribute to seed-harvesting in the Sonoran Desert (Hadley and Szarek 1981). A curved-billed thrasher is shown in Figure 14.10 consuming seeds and pulp of the fruit of a saguaro tree at 10:02 a.m., July 5, 2018. The vegetative part of the tree is protected from herbivory by spines, water loss by transpiration is reduced by the waxy surface under the spines, and the pleats of the saguaro enable it to grow larger or smaller with net uptake or loss of water.

Most saguaro seeds fall to the ground when the fruit drops, so an animal that can walk can eat the pulp and seeds, and a portion of the seeds, once consumed, pass through the digestive tract and are deposited with feces of the seed-dispersing animal. In the Sonoran Desert, the viability of seeds of saguaros that have been dispersed in the feces of animals that have consumed them will depend upon such stress factors as moisture, temperature, and protection from herbivory at locations where the seeds are deposited in the animal feces. Nonetheless, while not measuring the viability of dispersed



FIGURE 14.10 (See color insert.) Curve-billed thrasher (*Toxostoma curvirostre*) consuming seeds and pulp of the fruit of saguaro (*C. gigantea*). (Source: T W Crawford, Jr.)

TABLE 14.1
Viability of Saguaro Seeds from Feces of Several Mammalian and Avian Species

Species	Common Name	% Germination
<i>Canis latrans</i>	Coyote	97.0
<i>Pecari tajacu</i>	Javelina	31.0
<i>Spermophilus</i>	Round-tailed ground squirrel	64.2
<i>Citellus harrisi</i>	Harris's antelope squirrel	53.5
<i>Neotoma albigula</i>	White-throated wood rat	50.0
<i>Campylorhynchus brunneicapillus</i>	Cactus wren	76.0
<i>Toxostoma curvirostre</i>	Curve-billed thrasher	54.7
<i>Zenaida asiatica</i>	White-winged dove	100.0

seeds in the wild, laboratory testing of the relative viability of saguaro seeds found in different animal feces in low-stress, closed petri dishes at 22°C with uniform moisture supply indicates (Table 14.1) the relative benefits of animal consumption and dispersion of saguaro seeds (National Park Service 2005):

Eddy (1959) reported finding scat of *P. tajacu* in which 85% of the saguaro seeds were undigested, but he apparently did not test their germination. The data of Table 14.1 and Eddy's findings indicate that mammalian and avian consumers and dispersers of viable saguaro seeds can contribute to the survival of *C. gigantea*. However, stress on the saguaro seeds due to passing through the digestive tract of the seed dispersers can occur as seeds transit from the fruit to where they are consumed to the locations where the seeds come to rest as feces are deposited on the landscape. Survival of saguaro seeds at locations where they are dropped in animal feces may be increased if the seeds are protected by nurse plants away from stressful areas of intensive animal foraging at the base of fruiting saguaro plants. Such protected locations reduce stresses of herbivory and extreme temperatures, increasing the probability of seed survival and offering more suitable conditions for seed germination and seedling establishment (National Park Service 2005).

Mammals which exert the stress of herbivory on stems (pads) of *Opuntia* spp. (prickly pear) include *Odocoileus virginianus* (white-tailed deer) and *Pecari tajacu* (javelina). Prickly pear fruits are eaten by a wide range of birds and various omnivores such as *Canis latrans* (coyote), *Procyon lotor* (raccoons), among others (Russell and Felker 1987). Although most *Opuntia* spp. are nontoxic, they reduce the stress of herbivory by being able to injure herbivores with spines and glochids (Delfelice 2004). *Opuntia* stems generally contain high concentrations of oxalates that bind calcium and can lead to calcium deficiency. *N. albigula* (white-throated woodrat) that consumes *Opuntia* is able to do so by having microflora in its gut that can ferment and degrade structural carbohydrates such as oxalate (Justice 1985). Stress on *Opuntia* by herbivory of *Tayassu tajacu* (javelina or collared peccary) is selective, since the javelina prefers to eat stems (pads) that are lower in oxalate content and stems that have relatively short spines (Theimer and Bateman 1992). Testing using confined javelina and two different morphological types of *Opuntia* pads with spines removed, it was found that inner pads of the two morphological types had lower neutral detergent fiber, lower levels of calcium oxalate crystals and a higher percentage of water than the outer pads; the javelina preferred the inner pads. Comparing consumption of pads with long or short spines, the javelina preferred to eat the pads with the shorter spines. In contrast to the white-throated woodrat that has gut microorganisms that can degrade oxalate, javelina have developed feeding behavior to avoid, or at least minimize, consumption of *Opuntia*'s stressful chemical defense, oxalate.

L. tridentata has extremely complex chemical defenses to ward off the stresses of competition with other plants for water and to combat the stresses of herbivory. Based on their experimental data, Mahall and Callaway (1992) reported that the roots of *L. tridentata* inhibited elongation of the roots of either *L. tridentata* or *A. dumosa* in their vicinity. The allelopathy of *Larrea* roots may be a factor to help explain the distribution of *Larrea* plants.

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